

The Effects of Transcranial Direct Current Stimulation on Beat Perception Within the
Supplementary Motor Area

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Abstract

The association between music and movement in humans is thought to be the result of an overlap in the brain regions responsible for regulating movement and the brain regions responding to beat and rhythm. While various movement disorders are known to involve beat perception and timing, the mechanisms and structures underlying beat perception are not fully understood. This study investigates the role of the supplementary motor area (SMA), a motor region in the brain involved in beat perception. We hypothesized that an increase in SMA activity would result in improved beat perception while decreased SMA activity would result in a performance decrease in beat perception. Transcranial direct current stimulation was used to alter neural excitability within the SMA. Participants were randomly assigned to an anodal - increased excitability, or cathodal - decreased excitability condition. Participants then completed both a rhythm reproduction and discrimination task under controlled sham condition and their assigned excitability condition. Participants in both the anodal and cathodal stimulation condition did not perform significantly different compared to controls in both rhythm discrimination and reproduction tasks. These findings suggest that the SMA does not play a causal role in the perception of beat.

The Effects of Transcranial Direct Current Stimulation on Beat Perception Within the Supplementary Motor Area

Music and movement are intrinsically linked, throughout history humans have shown a natural tendency to respond to music through movement, whether it be through dance or simply tapping one's foot (Keller & Rieger, 2009). Evidentially, this movement isn't random, rather individuals move with very precise timing following consistent intervals. This type of movement is often described as following a beat, an underlying pulse that marks out equally spaced points in time (Cooper & Meyer, 1960). Few animal studies have been able to replicate the effect of beat perception and results have been limited with some evidence for beat perception in animals capable of vocal learning, such as some birds but not nonhuman primates (Patel, Iverson, Bregman, Schultz, 2009). Even within those species it is unclear whether they possess higher levels of rhythmic processing comparable to the level of humans suggesting that the ability to perceive a beat from rhythms is largely an ability unique to humans (Fitch, 2013). This is especially important to consider in clinical settings where animal models are critically important in modelling various behaviours and disorders. Patients with Parkinson's disease (PD) for instance experience significant impairments in beat perception in addition to their movement related deficits (Grahn & Brett, 2009). Understanding the mechanisms behind beat perception may yield key insights to the specialization of the human brain and disorders such as Parkinson's.

The two prevalent theories of timing, including motor and auditory timing, are the interval and entrainment models (Grahn, 2012). Interval models comprise of three separate components, an internal clock that measures duration, a reference memory which stores the duration, and a mechanism to compare new durations to the stored duration (Church &

Broadbent, 1990; Treisman, 1963). In the interval model, the activity of the internal clock depends on the onset of an external stimulus (Gibbon, 1977). The entrainment model suggests that rather than an internal clock, neural oscillators which generate peaks in amplitude at regular intervals are used as a reference in judgements of timing (Large & Jones, 1999). The period between peaks of these oscillations are then adjusted to match that of the stimulus. While there is still some disagreement over which theory serves as the better model, the entrainment model has had greater success in explaining how higher-level features of temporal patterns arise from neural oscillators of rhythmic stimuli.

While these models explain the process of timing, they don't necessarily explain why individuals are able to perceive a beat or pulse from various rhythmic stimuli. Individuals can perceive a beat from a temporal rhythmic sequence even without any nontemporal cues such as pitch, volume, and timbre (Brochard, Abecasis, Potter, Ragot, Drake, 2003). A key element for beat perception is the ratio relationship between intervals of a sequence. Intervals of integer ratio produce a stronger perception of beat where the smallest interval of the sequence can be encoded as the beat (Sakai et al., 1999). Studies on equitone intervals, sequences of identical tones, have also shown that individuals can spontaneously perceive accents causing certain notes to feel more prominent (Povel & Essens, 1985; Povel & Okkerman, 1981). In these sequences perceptual accents arise as a result of the temporal pattern of the sequence. Thus, a stronger beat may result when integer ratio intervals are formed into groups of consistent units, typically four in music, such that the perceptual accent is induced at the beginning of each group (Grahn & Brett, 2007).

Neuroimaging studies have shown the activation of several areas within the brain during rhythmic processing, including the basal ganglia, supplementary motor area (SMA), putamen,

mid-premotor cortex (PMC), dorsal premotor area (PMd), superior temporal gyrus (STG), and cerebellum (Chen, Penhune, & Zatorre, 2008; Grahn & Brett, 2007). These neuroimaging studies have shown that auditory brain regions are not the only areas involved in rhythmic processing and motor regions within the brain appear to also play a critical role. Many of these regions are also a part of the cortico-striatal-thalamic loop, a system of neural circuits thought to be key in facilitating beat-based timing through entrainment of neural oscillations (Rajendran, Harper, Garcia-Lazaro, Lesica, Schnupp, 2017; Teki, Grube, Kumar, Griffiths, 2011).

Grahn and Brett's (2007) study identified the basal ganglia and SMA as two key structures for beat perception within the cortico-striatal-thalamic loop. In the study participants were given rhythm reproduction and discrimination tasks with three forms of rhythms, metric-simple rhythms designed to elicit a strong beat, metric-complex rhythms designed to elicit a weak beat, and non-metric rhythms which elicit no beat. Functional magnetic resonance imaging (fMRI) showed that while many areas were active during rhythmic processing, only the basal ganglia and SMA had selectively increased activation for rhythms with a strong beat, suggesting that these two regions in the brain are involved in mediating beat perception. A follow up study found that patients with PD, a condition associated with basal ganglia impairment, performed significantly worse on strong-beat rhythm discrimination compared to controls, further supporting the basal ganglia as a crucial region for beat perception (Grahn & Brett, 2009).

The SMA, the latter of the two structures suggested to be involved in mediating beat perception, is a small area on the cortical surface of the brain, located in the medial aspect of the brain and anterior to the leg representation of the primary motor cortex. The SMA has been well documented to be involved in the facilitation of voluntary movement, planning of movement, and motor learning (Nachev, Kennard, & Hussain, 2008). The SMA has also been shown to be

involved in the sequence processing within various domains including spatial processing, numerical cognition, language, and music processing, implicating the SMA as a crucial structure for domain-general sequence processing (Cona & Semenza, 2017). As rhythms are by definition a sequence of temporal stimuli, it is highly likely the SMA plays a role in rhythm processing.

In the current study, transcranial direct current stimulation (tDCS), a safe and non-invasive brain stimulation technique, is used to alter activity of the SMA. Neurons must reach a threshold of potential difference between the inside and outside of the cell to generate action potentials. The weak current used in tDCS produces subthreshold changes that have a neuromodulatory effect on neurons rather than directly inducing action potentials (Dayan et al., 2013). Anodal tDCS depolarizes neurons, bringing the membrane potential closer to threshold, increasing the likelihood of target neurons firing. Oppositely, cathodal stimulation hyperpolarizes neurons bringing the membrane potential farther from threshold, decreasing the likelihood of target neurons firing. Previous studies have shown that the behavioural effects of a single session of tDCS are typically short lived, lasting for a maximum of a few minutes while there is some evidence for multiple, spaced sessions to increase the duration of these behavioural effects (Reis et al., 2009).

By manipulating the activity of the SMA, this study aims to extend upon the findings of the Grahn and Brett (2007) correlational study by providing causal evidence of SMA involvement in beat perception. It is hypothesized that the SMA is causally involved in the mediation of beat perception. Therefore, it is predicted increasing the excitability of the SMA should lead to improved performance on the rhythm discrimination and reproduction tasks while decreasing the excitability of the SMA should lead to decreased performance on rhythmic discrimination and reproduction tasks. We also predicted that changes in task performance under

tDCS would be most affected for strong beat rhythms where changes in beat perception would have the greatest impact.

Methods

Participants

Twenty-two undergraduate students (14M, 8 F), attending Western University were recruited for the study, one student was excluded from analysis as they did not complete stimulation. Participants were 18-20 years old ($M \approx 18.57$, $SD \approx 0.60$) and had an average of 3.1 years ($SD \approx 3.4$) experience playing a musical instrument. Participants were recruited through the psychology research participation pool, SONA, and were compensated 1 credit for each session completed for a maximum of 2 credits. All participants gave consent to participate and all study forms were approved by Western University's Research Ethics Board (REB).

To minimize any potential risk involving tDCS, participants were excluded from participating in the study if they had metallic implants, such as pacemakers, cerebral aneurysm clips or other electronic implant, if they have a history of psychiatric or neurological problems such as epileptic seizures, Tourette's syndrome, ADHD, depression, if they require prescribed psychotropic medication or currently take other medication that makes them drowsy, if they get migraines and/ or are susceptible to headaches, and if they were more susceptible to skin irritation, such as participants with eczema. Female participants who are pregnant, trying to conceive, or who are sexually active and are not practicing an effective method of contraception were also excluded from participating in the study.

Stimuli

Three types of rhythms were used in the rhythmic discrimination task: metric-simple rhythms, metric-complex rhythms, and non-metric rhythms. These rhythms were chosen such that the perceptual accents form a perceived strong beat, weak beat, or no beat respectively (Grahn & Brett, 2007). The rhythms were generated with no differences in either volume or pitch. In the metric conditions, the durations of intervals were analogous to whole-integer ratios (1 : 2 : 3 : 4). In the non-metric condition, some interval durations were jittered so that they were not integer ratios (1 : 1.4 : 3.6 : 4). The base interval of 1 in each rhythm, representing the smallest time interval between auditory stimuli, was randomly selected between 225ms, 250ms, or 275ms to control for effects of tempo. Each rhythm consisted of 5 to 7 intervals with the integer ratios of all metric intervals adding up to 12 (see Appendix A).

The rhythms were all balanced such that each unique interval (e.g., 1, 2, 3, or 4) appeared a similar number of times across all rhythm conditions. The rhythms were also balanced such that the average error for each rhythm type was consistent with the average error found in previous studies. Rhythms on which individuals performed abnormally high or low were not included in the rhythm list used for the task.

Metric-simple rhythms were generated such that the intervals of integer ratio produced perceptual accents at the beginning of each group of four units. These rhythms were designed to elicit a perceived strong beat (see Figure 1).

Metric-complex rhythms were generated such that the intervals of integer ratio produced perceptual accents that did not coincide with groups of four units. These rhythms were designed to elicit a weak beat (see Figure 1).

Non-metric rhythms were generated from the metric-complex rhythms such that the integer ratios of the metric-complex rhythms (1 : 2 : 3 : 4) were transformed to non-metric integer ratios (1 : 1.4 : 3.6 : 4). These rhythms were designed such that they did not elicit the perception of a beat (see Figure 1).

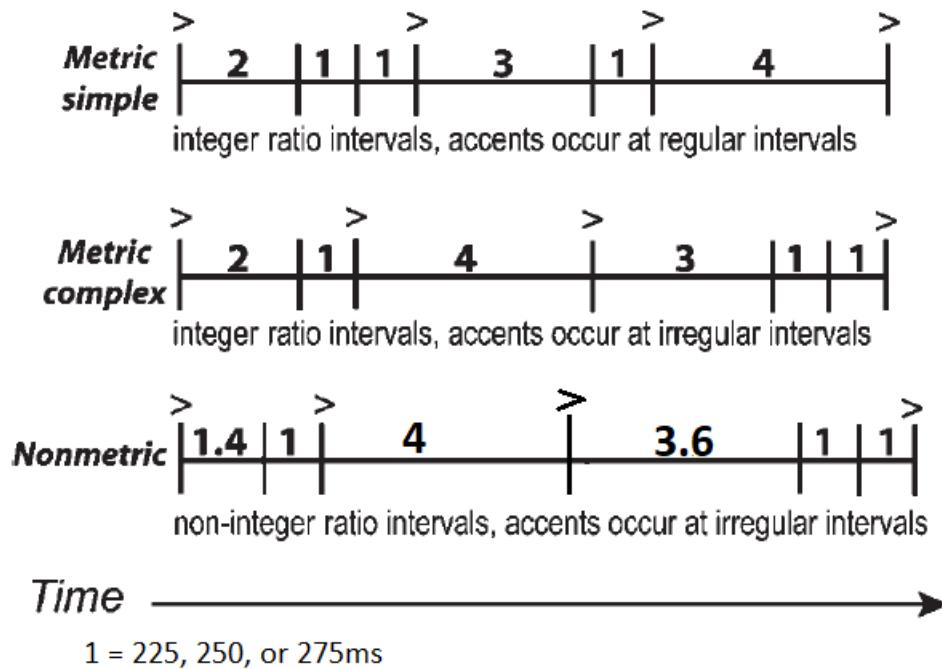


Figure 1. Schematic of sample stimuli. Vertical bars indicate interval onset, ‘>’ indicate where perceptual accents should be heard (Povel & Okkerman, 1981). Adapted from Grahn & Brett (2007).

Tasks

Two different tasks were used to assess participants' ability to discriminate between and reproduce rhythms. The rhythm discrimination task consisted of 60 trials, 20 trials from each of the three rhythm conditions. The order of rhythms being presented in each task were randomized such that participants did not experience the same order of rhythms to minimize sequence effects. Participants first practiced each task with 2 unique trial rhythms until they were

comfortable with the controls before beginning each task. The tasks were run using E-Prime software and the rhythms were delivered binaurally through headphones.

In the rhythm discrimination task participants listened to a randomly selected rhythm twice. Participants then listened to a third rhythm which could either be the same as the rhythm they had just heard or a slightly altered rhythm in which the interval order near the middle of the rhythm was switched (e.g., 1 3 3 1 2 2 to 1 3 1 3 2 2). Participants were then asked to tap either the ‘1’ key on the computer if they believed it was the same rhythm or the ‘0’ key on the computer if they believed it was a different rhythm. This was repeated until participants completed 60 trials or all 60 of the rhythms. There were equal number (30) of ‘same’ and ‘different’ rhythm trials.

In the rhythm reproduction task participants listened to a randomly selected rhythm twice. Participants were then asked to tap back each interval onset in the rhythm using the ‘m’ key on the computer. This was repeated until participants completed 60 trials or all 60 of the rhythms.

Transcranial Direct Current Stimulation (tDCS)

In this study the Chattanooga Ionto Dual Channel Electrophoresis System was used to apply 2mA of current to the electrodes performing the tDCS. Two electrodes were placed on the participants’ head using the 10-20 system typically used for electrode placement in electroencephalogram (EEG) (DaSilva, Volz, Bikson, Fregni, 2011). Participants’ heads were measured from the naision, the point between the forehead and nose, and the inion, most prominent point of the occipital bone. The inter-auricular distance from in front of one ear to in front of the other was also measured. The intersection of the two measurements is the vertex. To

target the SMA, the target electrode (e.g., the anodal electrode if the participant was to receive anodal stimulation) was placed 2cm rostral to the vertex and the reference electrode was placed on the forehead above the right eye.

Experimental Procedure

Upon arriving for the first session of the study, participants were informed of the task and signed a letter of consent. Participants were then randomly assigned to receive either anodal or cathodal stimulation and one of either the rhythm discrimination task or the rhythm reproduction task (see Figure 2). Before beginning the task, the tDCS electrodes were placed in saline soaked sponges that increased conductivity and then placed onto the correct positions on the participant's head. More saline was added if participants experienced any discomfort.

Participants began their assigned task in the sham condition in which the tDCS was ramped up to 2mA over a few seconds before being ramped back down to zero. The task lasted for approximately 20 minutes and after completing the task, subjects repeated the task in their assigned stimulation condition. At the end of session one, subjects were asked to complete a demographics questionnaire. In session two, subjects were assigned to receive the same stimulation they had received in the previous session and the other of the two tasks. Participants again began their assigned task in the sham condition and repeated the task in the stimulation condition. At the end of session two, subjects were asked whether they noticed the presence of the sham condition, they were then debriefed and made aware the presence of the sham condition. Sessions were scheduled at least a day apart to ensure there were no residual tDCS effects.

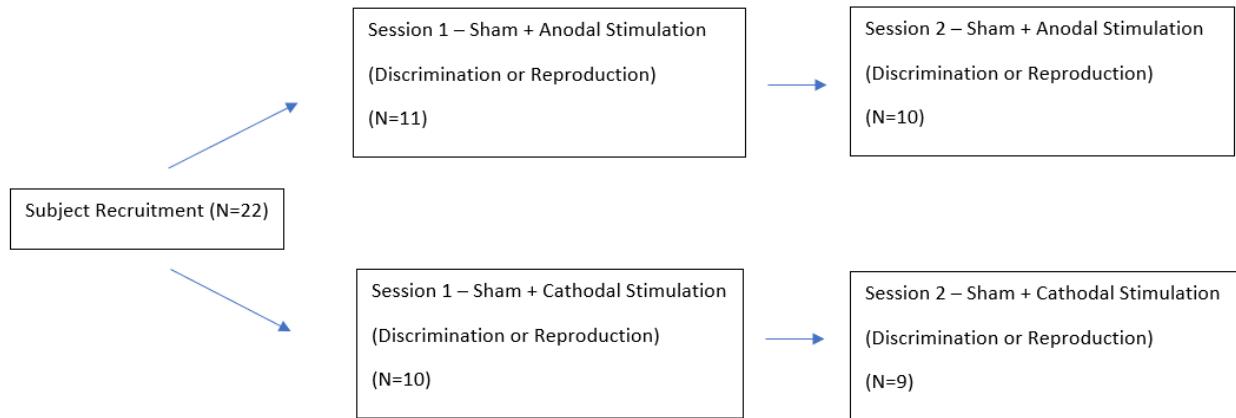


Figure 2. Study design of experiment. Anodal or Cathodal Stimulation was randomly assigned to each participant. The rhythm discrimination and reproduction tasks were randomly assigned to either session 1 or session 2 for each participant. Sessions 1 and 2 were completed on two separate days.

Data Analysis

Performance on the reproduction task was measured as average proportion error where the difference in time from an individual's input and the time of the correct input, error, was converted to a proportion where 0 represents that the individual had reproduced the intervals perfectly in sync with the actual interval. These proportions were then averaged for all rhythm trials of the task. Performance on the discrimination task was measured by the proportion of incorrect trials. Each correct response during the task was recorded and the total number of correct responses was converted to a proportion where 1 represents inputting the correct response for every rhythm of the discrimination task. These values were then subtracted from 1 to generate the proportion of incorrect trials such that the measures of performance were in the same direction for both tasks, lower values representing a better performance.

All graphs were generated in Microsoft Excel and data analysis was conducted in SPSS.

Two separate 2 (Sham vs Stimulation) x 2 (Cathodal vs Anodal) x 3 (Metric-Simple vs Metric-Complex vs Non-Metric) mixed measures analysis of variances (ANOVA) were used to

analyze the main effects of presence of stimulation, type of stimulation, type of rhythm, and their interactions, 1 ANOVA for each of the two tasks. The presence of stimulation and type of rhythms were tested within subjects and the type of stimulation was tested between subjects.

A pairwise comparisons test was conducted as a follow up to analyze conditions that had either a significant main effect or were approaching significance.

An independent samples test was also conducted as a planned analysis on the difference scores of each task. Difference scores were generated as another value intended to measure the effects of stimulation. They calculated the absolute value, to account for directionality of the stimulation type, of the difference between an individual's performance on a task pre and post receiving tDCS.

Correlations were generated between an individual's performance on each task, matched for presence of stimulation and rhythm type. These correlations were intended to measure how strongly an individual's performance on one task predicted their performance on the other.

Results

Reproduction Task

A 2 (Sham vs Stimulation) x 2 (Cathodal vs Anodal) x 3 (Metric-Simple vs Metric-Complex vs Non-Metric) mixed measures ANOVA was used to test for the effects of presence of stimulation (Sham vs Stimulation), rhythm type (Metric-Simple vs. Metric-Complex vs. Non-Metric), and stimulation type (Anodal vs. Cathodal) on performance in the rhythm reproduction task (see Figure 3). Results showed a significant main effect of rhythm type on task performance ($F(2, 34) = 7.332, p = 0.002$) however no interaction effect was found between the type of rhythm and type of stimulation ($F(2, 34) = .380, p = .686$). No significant main effect was found for presence of stimulation on task performance ($F(1, 17) = 1.325, p = .266$) and no interaction

effect was found between the presence of stimulation and type of stimulation ($F(1, 17) = .748, p = .399$). No interaction effects were found between the rhythm type and presence of stimulation ($F(2, 34) = 1.479, p = .242$) or between the three way interaction of rhythm type, presence of stimulation and stimulation type ($F(2, 34) = .320, p = .728$). Mauchly's Test of Sphericity was conducted and none of the conditions violated the sphericity assumption.

A follow up pairwise comparisons test was conducted looking at the main effect of rhythm type. The pairwise comparisons showed that there was a significant difference in performance between metric-simple (MS) rhythms and metric-complex (MC) rhythms ($t = -3.667, p = .002$) and between metric-simple (MS) rhythms and non-metric (NM) rhythms ($t = -2.950, p = .009$). No significant difference was found between metric-complex (MC) rhythms and non-metric (NM) rhythms ($t = .114, p = .911$).

An independent samples test was conducted on the difference scores to assess effects of stimulation on performance in the reproduction task (see Figure 3). No significance was found in the metric-simple difference scores ($t = -.544, df = 17, p = .587$), the metric-complex difference scores ($t = .306, df = 17, p = .763$) and the non-metric difference scores ($t = -.884, df = 17, p = .389$). Levene's Test for Equality of Variances was conducted and none of the conditions violated the equal variances assumption.

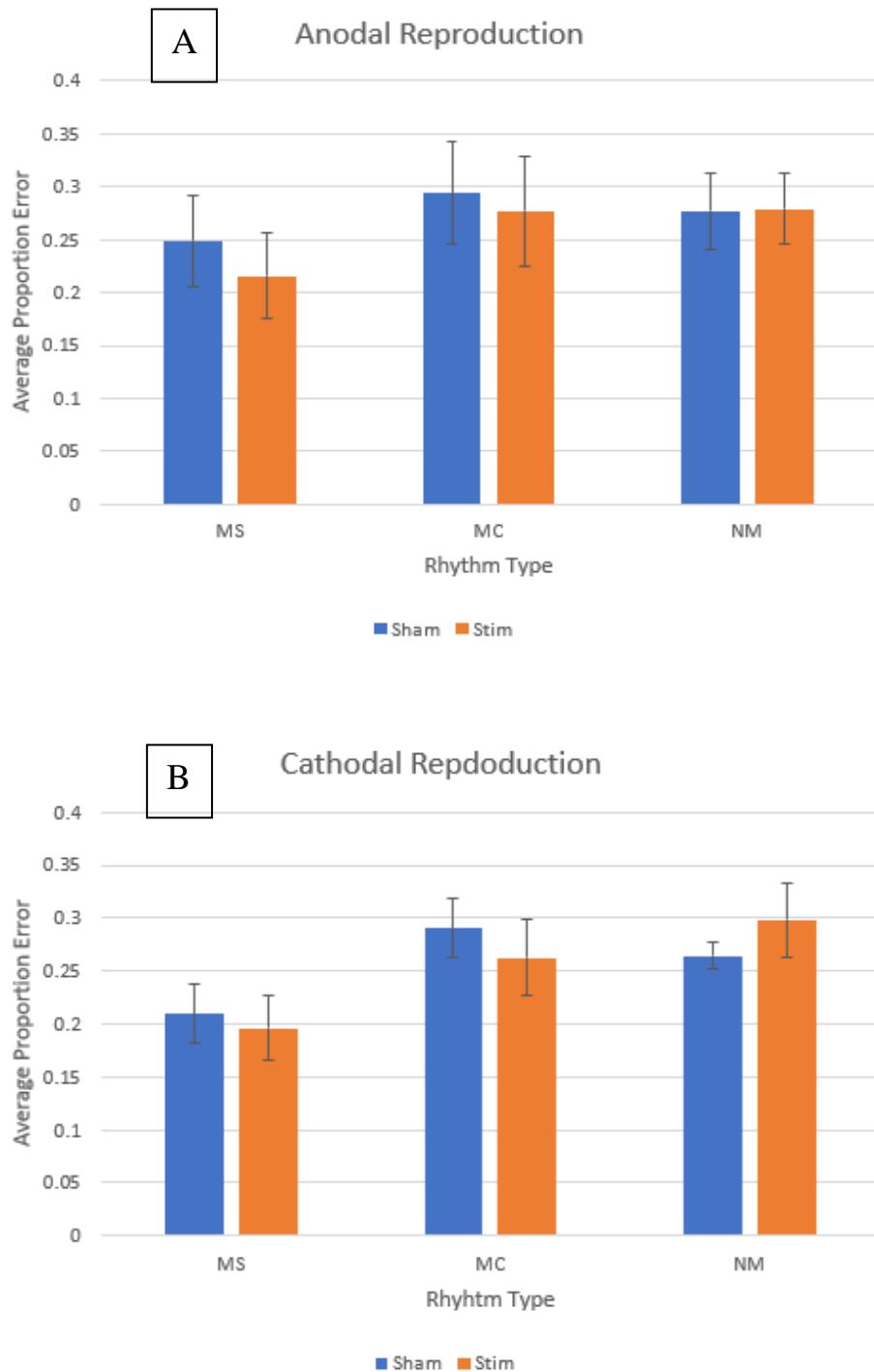


Figure 3. Average proportion error as a measure of performance on the rhythm reproduction task on Metric-Simple (MS), Metric-Complex (MC), and Non-Metric (NM) rhythms during sham (blue) condition and stimulation (orange) condition in both anodal (A) and cathodal (B) stimulation groups.

Discrimination Task

A 2 (Sham vs Stimulation) x 2 (Cathodal vs Anodal) x 3 (Metric-Simple vs Metric-Complex vs Non-Metric) mixed measures ANOVA was used to test for the effects of presence of stimulation (Sham vs Stimulation), rhythm type (metric-simple vs. metric-complex vs. non-metric), and stimulation type (Anodal vs. Cathodal) on performance in the rhythm discrimination task (see Figure 4). Results showed no significant main effect of rhythm type on task performance ($F(2, 36) = 2.848, p = .071$) and no interaction effect was found between the type of rhythm and type of stimulation ($F(2, 36) = 1.076, p = .352$). No significant main effect for the presence of stimulation on task performance ($F(1, 18) = .093, p = .763$) was found and no interaction effect was found between the presence of stimulation and type of stimulation ($F(1, 18) = .093, p = .763$). No interaction effects were found between the rhythm type and presence of stimulation ($F(2, 36) = 2.513, p = .095$) or between the three way interaction of rhythm type, presence of stimulation and stimulation type ($F(2, 36) = .230, p = .796$). Mauchly's Test of Sphericity was conducted and none of the conditions violated the sphericity assumption.

A follow up pairwise comparisons test was again conducted to analyze the main effect of rhythm type. The pairwise comparisons showed that there was a significant difference in performance between metric-simple (MS) rhythms and metric-complex (MC) rhythms ($t = -2.465, p = .023$). No significant difference was found between metric-simple (MS) rhythms and non-metric (NM) rhythms ($t = -.843, p = .410$) or between metric-complex (MC) rhythms and non-metric (NM) rhythms ($t = 1.350, p = .193$).

An independent samples test was conducted on the difference scores to assess effects of stimulation on performance in the discrimination task (see Figure 4). No significance was found in the metric-simple difference scores ($t = -.272, df = 18, p = .789$), the metric-complex

difference scores ($t = .729$, $df = 11.793$, $p = .480$) and the non-metric difference scores ($t = .095$, $df = 18$, $p = .925$). Levene's Test for Equality of Variances was conducted and equal variances not assumed values were used for conditions that tested significant on the Levene's Test.

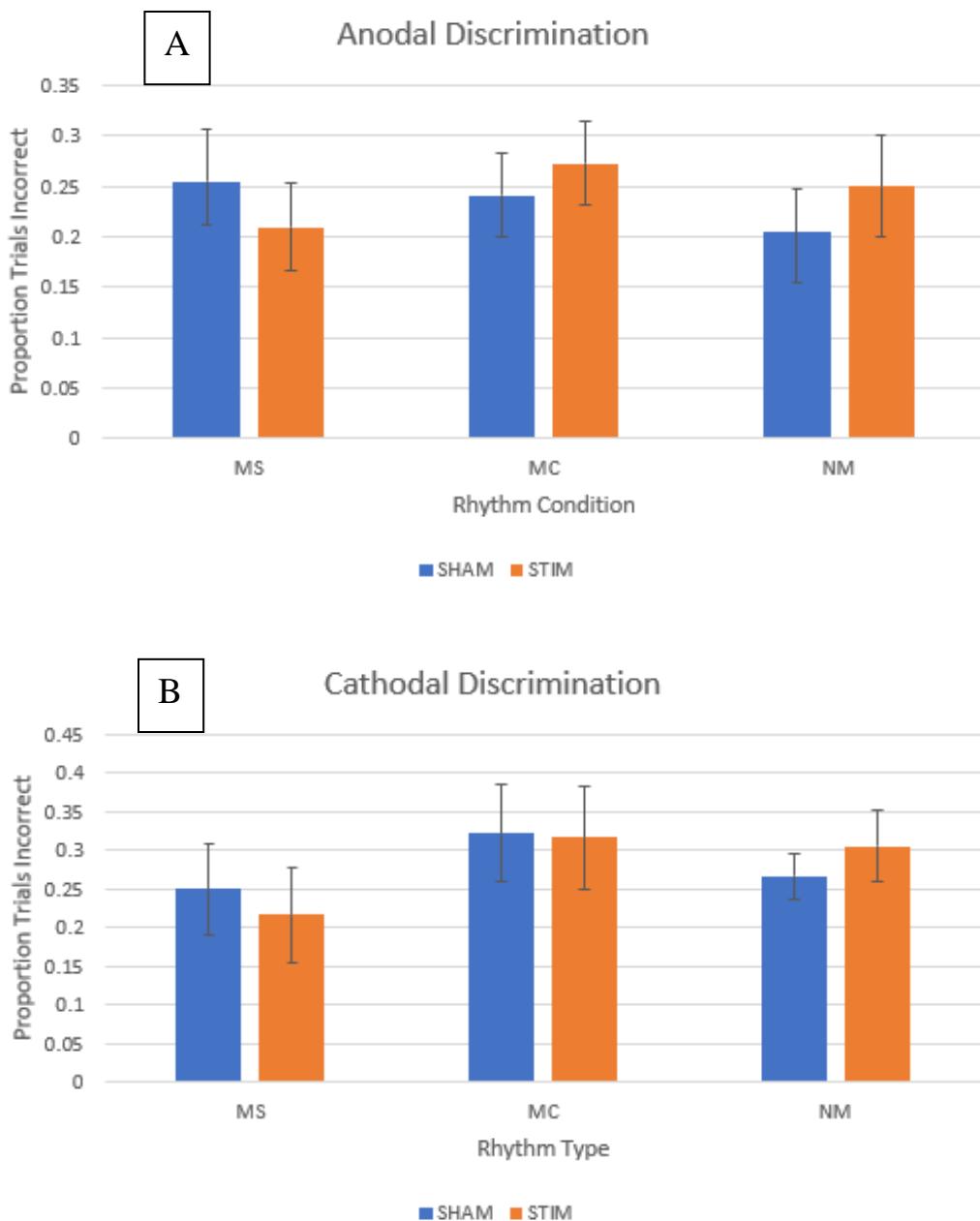
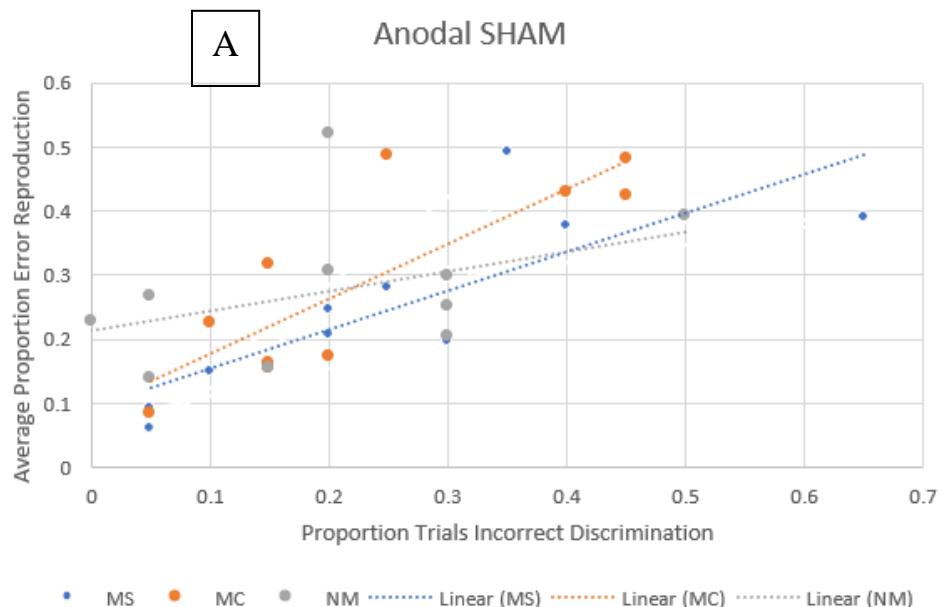
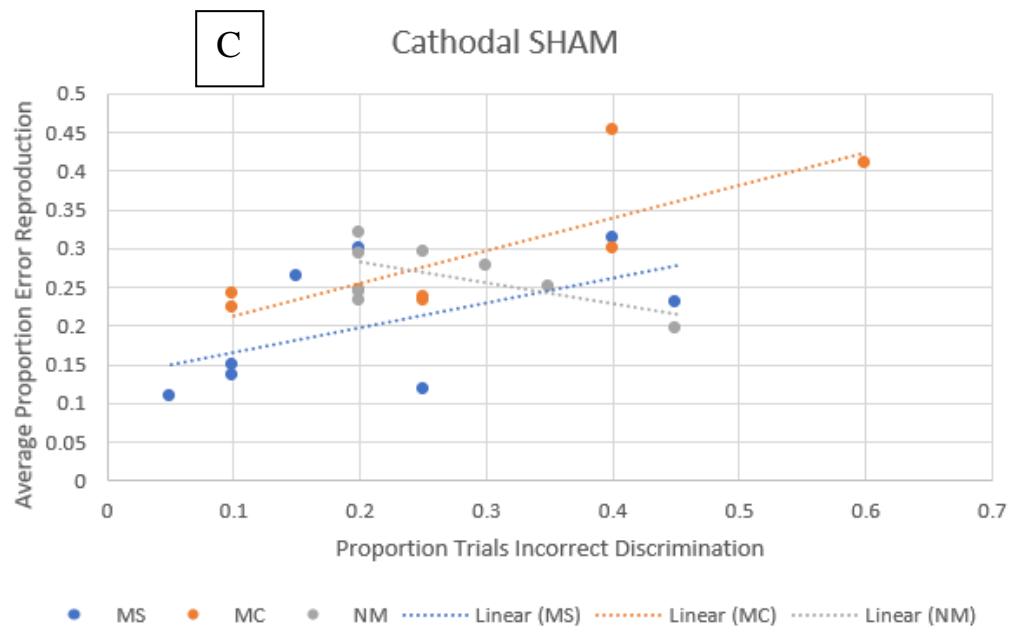
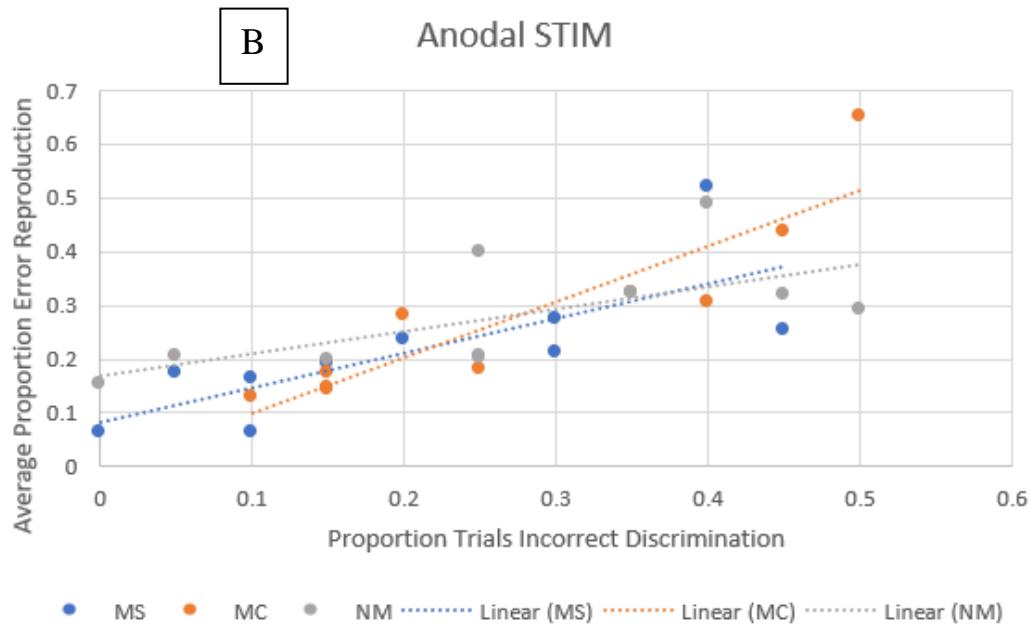


Figure 4. Proportion of trials incorrect as a measure of performance on the rhythm discrimination task on Metric-Simple (MS), Metric-Complex (MC), and Non-Metric (NM) rhythms during sham (blue) condition and stimulation (orange) condition in both anodal (A) and cathodal (B) stimulation groups.

Task Correlations

SPSS was used to analyze the correlational strength between an individual's performance on the reproduction task and their performance on the discrimination task (see Figure 5). A relative strong correlation was found between an individual's performance on metric-simple rhythms between reproduction and discrimination tasks in both no stimulation ($r = .740, p < .001$) and stimulation ($r = .662, p = .003$) conditions. Similar correlations were found between an individual's performance on metric-complex rhythms between reproduction and discrimination tasks in both no stimulation ($r = .768, p < .001$) and stimulation ($r = .800, p < .001$) conditions. A relatively weaker, non-significant correlation was found between an individual's performance on non-metric rhythms between reproduction and discrimination tasks in the no stimulation condition ($r = .234, p = .350$) and a slightly stronger correlation was found in the stimulation condition ($r = .563, p = .015$).





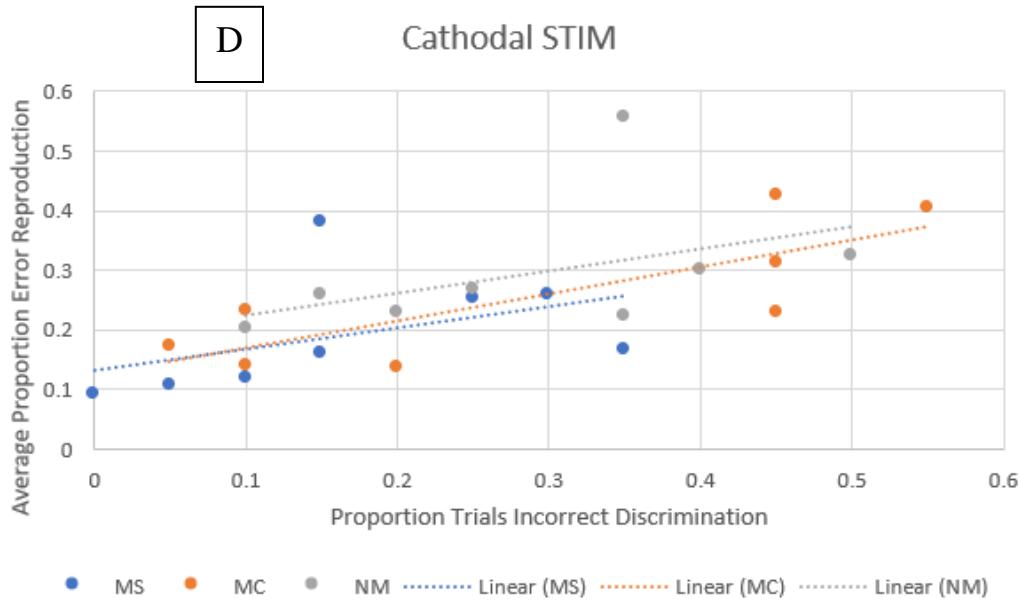


Figure 5. Performance on the discrimination task (proportion trials incorrect) correlated against performance on the reproduction task (average proportion error) for Metric-Simple (MS), Metric-Complex (MC), and Non-Metric (NM) rhythm types. A linear line of best fit was fit to each rhythm type. A) No stimulation, anodal group. B) Anodal stimulation group. C) No stimulation, cathodal group. D) Cathodal stimulation group.

Discussion

The results from the mixed measures ANOVA revealed that there was a significant main effect of the type of rhythm (beat strength) on performance in the reproduction task but not the discrimination task. These findings are somewhat inconsistent with previous literature which have suggested that individuals tend to perform better on metric-simple or strong beat rhythms in both reproduction and discrimination tasks (Grahn & Brett, 2007; Grahn & Brett, 2009). The inconsistency could potentially be due to a relatively weaker sample size as the main effect of rhythm type in the discrimination task appears to approach significance. A follow up pairwise comparisons test confirmed that individuals performed significantly better on metric-simple rhythms compared to both metric-complex and non-metric rhythms in the reproduction task. In the discrimination task individuals performed significantly better on the metric-simple rhythms

compared to metric-complex but not non-metric rhythms. The pairwise comparisons showed that some of the expected effects of rhythm type on performance were still present in the discrimination task and it is possible that a larger sample size was needed to elucidate all effects.

The ANOVA also revealed no main effects of either the type of stimulation or the presence of the stimulation itself. Similarly, no interaction effects were found between the type of rhythm, presence of stimulation, or type of stimulation. The follow up independent samples test conducted on individuals' difference scores also found no significance in the difference scores across both tasks and all three rhythm types. These findings are contrary to the hypothesis and suggest that stimulation of the SMA had relatively no impact on an individual's beat perception ability. Numerically, a non-significant improvement in performance was observed from pre-stimulation to post-stimulation on the metric-simple and metric-complex rhythms across both stimulation types and both tasks (see Figures 3 and 4) suggesting a possible practice effect between their first and second run through of a task.

An additional analysis was conducted to investigate the correlation between an individual's performance on the two tasks. We anticipated that the two tasks would be strongly correlated as they were both measures of one's beat perception ability. The findings revealed that the correlations in performance between both tasks were stronger when the rhythm was either a metric-simple or metric-complex rhythm and weaker for non-metric rhythms. This was relatively expected as metric-simple and metric-complex rhythms both utilize one's beat perception ability while performance on the non-metric rhythms across tasks could be less consistent as the rhythm is intended to not induce the perception of a beat, thus performance would be less correlated with one's beat perception ability.

As a whole, the results of the current study do not support the original hypothesis. It was predicted that altering the excitability of one's SMA would alter one's beat perception ability and performance on tasks utilizing beat perception. This alteration was expected to depend on both the type of stimulation as well as the strength of the perceived beat from the rhythm. Although the strength of beat perceived in the rhythm did play a role in influencing one's performance, there were no significant effects or interactions relating to the presence or type of stimulation in either the reproduction or discrimination tasks. These findings suggest that contrary to expectations, the SMA does not play a causal role in the mediation of beat perception.

As previously mentioned, Grahn and Brett's (2007) study had shown correlational evidence implicating the SMA's involvement in beat perception. The results from this study do not support these previous findings and suggests that while the SMA may be correlated in some way to an individual's beat perception ability, that the SMA is not the main brain structure responsible for mediating beat perception.

One potential explanation for this could be that the SMA's involvement in auditory processing is limited to rhythmic sequence processing. Cona and Semenza's (2017) review on the SMA's involvement in sequence processing highlighted that the region was consistently activated in tasks involving sequence processing across several domains, auditory and rhythmic sequencing being one of them. Their review strongly implicates that the SMA functions on a domain general level suggesting that while the SMA could be necessary in processing the rhythm of an auditory stimulus, it is not directly involved in generating the perceived, underlying beat.

It is also important to consider that the SMA is only one component of the cortico-striatal-thalamic loop, sometimes also referred to as the cortico-basal-ganglia-thalamocortical loop. This loop consists of a system of neural circuits within the brain involving connections

between the cortex, including the SMA and motor cortices, the basal ganglia, and thalamus. Previous studies have suggested that the cortico-striatal-thalamic loop is involved in the facilitation of beat-based timing (Kotz, Brown, Schwartze, 2016; Teki, Grube, Kumar, Griffiths, 2011). The basal ganglia in particular was previously shown to play a crucial role in perceptual timing and was the other structure in the Grahn and Brett (2007) imaging study implicated to be involved in beat perception. In a later study conducted by Grahn and Brett (2009), they tested patients with Parkinson's disease (PD), a disorder marked by degeneration within segments of the basal ganglia and motor impairment, on a rhythm discrimination task and found that their ability to perceive beat appeared to be impaired as they performed significantly worse compared to controls on metric-simple rhythms but not metric-complex rhythms. Other studies conducted with PD patients have also suggested that the basal ganglia plays a role in facilitating both motor and perceptual timing (Boyle, Freeman, Cody, 1996; Grahn, 2009; Jones & Jahanshashi, 2014).

Another finding implicating the importance of the basal ganglia is that several neural pathways have been found linking the basal ganglia with both cortical regions such as the SMA, and the cerebellum (Bostan, Dum, Strick, 2013). One relatively new theory that has been suggested is that beat perception and timing may be a result of the interplay between the regions and networks of the cortico-striatal-thalamic loop as a whole, made possible by the connections to the basal ganglia, as opposed to the function of a single brain structure (Merchant, Harrington, Heck, 2013; Teki, Grube, Griffiths, 2012).

Limitations

One limitation of the study pertains to the effectiveness of tDCS itself. Although some recent studies have been able to demonstrate significant effects of tDCS on similar motor regions, such as within the dorsolateral premotor cortex (Pollok, Overhagen, Keitel, Krause,

2017), other groups are still concerned over the effectiveness and precision of tDCS usage (Chrysikou, Berryhill, Bikson, Coslett, 2017). For instance, at the time of conducting this study, there is no set standard for the amount of tDCS to be used on a participant although 2mA for 5 to 30 minutes appears to be most common (Thair, Holloway, Newport, Smith, 2017). It is also unclear what the most effective dosage of tDCS should be for the SMA as effective dosages could be different for various regions of the brain and there have been relatively mixed findings in previous studies that have utilized tDCS to test the SMA (Carlson, Eagles, MacKinnon, 2015; Hupfeld, Ketcham, Scheider, 2017; Lu, Amundsen, Tuite, MacKinnon, 2018).

Additionally, the sample size of the current study was slightly lower than what we had aimed for as testing time was cut short due to current world circumstances.

Future Research

Future studies should further investigate the basal ganglia and the cortico-striatal-thalamic loop. While there has been a great deal of evidence implicating the basal ganglia's involvement in beat perception and timing, currently there is no causal evidence confirming that the basal ganglia is directly mediating beat perception. Future research should aim to investigate individuals with isolated impairments in the basal ganglia as opposed to individuals with PD who experience multiple deficits in addition to basal ganglia degeneration. Additionally, understanding of how the cortico-striatal-thalamic loop is involved in beat processing is still relatively new and continued research should aim to understand how the interplay between various networks contributes to beat perception and whether beat perception is a function specific to one component within the loop or a function of the loop as a whole.

Another future research project that could address concerns regarding the effectiveness of tDCS is to conduct a similar study using a repeated tDCS model. It has been known that repeated doses of tDCS tend to produce stronger effects with an extended duration compared to single session doses of tDCS but there have been concerns regarding the safety of repeated doses (Thair, Holloway, Newport, Smith, 2017). Some recent evidence has implicated that repeated sessions of tDCS do not pose an increased risk to participants in comparison to single session doses (Nikolin et al., 2018) suggesting that it may be a more effective way to administer tDCS.

Conclusions

The results of the current investigation were unable to support previous findings suggesting that the SMA is causally involved in mediating beat perception. Instead they suggest that while SMA activity may be correlated with beat perception, the SMA itself is not the area responsible for mediating beat perception. These findings contribute to the relatively new area of understanding beat perception in relation to the cortico-striatal-thalamic loop. Continued research is encouraged to further the understanding of the other components and interactions of the cortico-striatal-thalamic loop, notably the basal ganglia which had previously been implicated to mediate beat perception. Gaining a better understanding of the mechanisms underlying our beat perception abilities will further our understanding of the human brain and potentially allow for us to develop new interventions to treat disorders such as PD that involve impairments to beat and timing processes.

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Appendix A

A table listing the rhythm sequences used for each condition

Interval Sequence	Rhythm Type
1 1 3 2 1 3 1	Metric-Complex
1 2 2 1 4 2	Metric-Complex
1 2 4 1 1 3	Metric-Complex
1 3 2 4 2	Metric-Complex
2 1 4 1 2 1 1	Metric-Complex
2 1 4 3 1 1	Metric-Complex
2 2 1 2 4 1	Metric-Complex
2 3 1 1 2 3	Metric-Complex
4 1 2 2 1 2	Metric-Complex
4 1 2 3 2	Metric-Complex
3 3 1 4 1	Metric-Complex
3 2 3 2 1 1	Metric-Complex
4 2 1 3 1 1	Metric-Complex
2 1 4 2 2 1	Metric-Complex
3 2 1 4 1 1	Metric-Complex
1 1 1 2 4 1 2	Metric-Complex
3 1 1 3 1 2 1	Metric-Complex
4 1 1 1 2 2 1	Metric-Complex
2 3 3 1 1 1 1	Metric-Complex
1 1 3 2 2 1 2	Metric-Complex
1 1 2 3 1 4	Metric-Simple
2 1 1 2 2 3 1	Metric-Simple
2 2 1 1 1 1 4	Metric-Simple
2 2 2 1 1 4	Metric-Simple
3 1 2 1 1 1 3	Metric-Simple
3 1 2 2 1 1 2	Metric-Simple
3 1 4 1 3	Metric-Simple
3 1 4 2 2	Metric-Simple
4 1 1 2 3 1	Metric-Simple
4 2 2 1 1 2	Metric-Simple
4 1 3 3 1	Metric-Simple
2 2 3 1 1 3	Metric-Simple
2 1 1 4 1 3	Metric-Simple
3 1 1 3 2 2	Metric-Simple
3 1 2 2 1 3	Metric-Simple
1 1 1 1 4 3 1	Metric-Simple
1 1 2 2 1 1 4	Metric-Simple
1 1 2 3 1 2 2	Metric-Simple
2 1 1 3 1 1 3	Metric-Simple

1 1 2 3 1 1 3	Metric-Simple
1 1 3.6 1.4 1 3.6 1	Non-Metric
1 1.4 1.4 1 4 1.4	Non-Metric
1 1.4 4 1 1 3.6	Non-Metric
1 3.6 1.4 4 1.4	Non-Metric
1.4 1 4 1 1.4 1 1	Non-Metric
1.4 1 4 3.6 1 1	Non-Metric
1.4 1.4 1 1.4 4 1	Non-Metric
1.4 3.6 1 1 1.4 3.6	Non-Metric
4 1 1.4 1.4 1 1.4	Non-Metric
4 1 1.4 3.6 1.4	Non-Metric
3.6 3.6 1 4 1	Non-Metric
3.6 1.4 3.6 1.4 1 1	Non-Metric
4 1.4 1 3.6 1 1	Non-Metric
1.4 1 4 1.4 1.4 1	Non-Metric
3.6 1.4 1 4 1 1	Non-Metric
1 1 1 1.4 4 1 1.4	Non-Metric
3.6 1 1 3.6 1 1.4 1	Non-Metric
4 1 1 1 1.4 1.4 1	Non-Metric
1.4 3.6 3.6 1 1 1 1	Non-Metric
1 1 3.6 1.4 1.4 1 1.4	Non-Metric
